

LIANAS AND HEMIEPIPHYTES: DISTRIBUTION, DEVELOPMENT, AND ADAPTATIONS

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ABSTRACT. Although poorly known and often neglected life forms, lianas and hemiepiphytes are frequently found in tropical canopies. Lianas (such as rattans) and hemiepiphytes (such as *Ficus*) are specialized life forms of the canopy that share a number of similarities, including spatial conditions and the requirement of a host plant. To better understand the biology of lianas and hemiepiphytes, the authors, during a 15-year period (1985–2000), collected data to compare several aspects of these two groups: geographic and taxonomic repartition, seedling and establishment phases, architectural development, and vegetative propagation. Considering the prevalence of lianas and hemiepiphytes in tropical canopies, the authors discuss the response of these plants to environmental conditions and speculate on their role in forest dynamics.

Key words: ecology, growth strategy, hemiepiphyte, liana, plant architecture, taxonomic distribution

INTRODUCTION

In tropical forests, lianas generally are associated with more or less disturbed areas. Although hemiepiphytes may also be found growing here, they are most frequent in undisturbed primary forest (Putz 1985, Balée & Campbell 1990, Hegarty & Caballé 1991, Phillips & Gentry 1994, Pinard & Putz 1994). Liana and hemiepiphyte floristic diversity can represent up to 20–25% of the vascular flora (Gentry & Dodson 1987, Gentry 1991). Their presence and abundance can reach surprisingly high percentages: up to 85% of forest trees can act as supports for lianas (Putz 1984a, Clark & Clark 1990, Campbell & Newbery 1993, Pérez-Salicrup 1998), and about 20% of forest trees have been reported as colonized by hemiepiphytes (Prósperi 1998a).

The study of these specialized life forms can be difficult, and thus the growth of knowledge relating to them has been hampered. In the field, lianas and hemiepiphytes are not always immediately recognizable in part or entirely; further, in the canopy they may be integrated into tree crowns. Recognition of a young hemiepiphyte in the canopy can be very difficult and may require detailed observation. Similarly, depending on the developmental stage, lianas or hemiepiphytes may be confused with other biological types. In the understory, the self-supporting stage of a liana, such as *Hugonia* (Linaceae), may be mis-

taken for a young tree, leading to errors in forest inventories (Caballé 1986, 1998). Many such errors stem from inadequate knowledge of the different ontogenetic stages of lianas and hemiepiphytes.

Woody lianas and hemiepiphytes occupy a prominent place in forest ecosystems and may reach over-all sizes and heights similar to canopy trees (Putz 1995, Williams-Linera & Lawton 1995). To become established and grow in the canopy, lianas and hemiepiphytes use modes of development not principally associated with trees. In particular, the growth pattern of these organisms differs considerably from that of trees, and the properties of their specialized development allow them to exploit the forest ecosystem with considerable success.

Increasingly lianas and hemiepiphytes are included in studies of forest ecology and dynamics (Michaloud & Michaloud-Pelletier 1987, Lowman & Nadkarni 1995, Putz & Mooney 1991). Few in-depth studies, however, have been made of the biology of lianas and hemiepiphytes, most contributions being limited to mention of their presence in floristic treatments or as part of demographic parameters in ecological studies.

The objectives of our study were to better understand the special attributes that allow lianas and hemiepiphytes to evolve in the context of a forest, as well as to begin to construct hypotheses regarding their respective roles in forest structure and dynamics. Our study compared geographical distribution and taxonomic repar-

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tition and gathered new information regarding their development of these forest canopy inhabitants.

MATERIAL AND METHODS

We restrict our discussion to woody species of lianas and hemiepiphytes, as only these attain the dimensions of large trees. We further define lianas as woody climbing plants that start their life on the ground, are not self-supporting except when young or facing a special constraint, and whose reproductive phase occurs in sunlight. Woody hemiepiphytes are defined as plants that begin their life on a tree and secondarily reach the ground by means of roots (Schimper 1888). We exclude plants of small stature such as *Medinilla* (Melastomataceae) or *Illia* (Rubiaceae). The trait of beginning life in a tree also excludes plants named "secondary hemiepiphytes," such as Cyclanthaceae, Marcgraviaceae, or some Araceae (see Williams-Linera & Lawton 1995). Rooting in the soil is, for hemiepiphytes, a necessary condition for development of sexual maturity and attainment of dimensions comparable to emergent trees. Characteristically, hemiepiphytes, from juvenile stages onward, express a strongly developed adventitious root system.

Previous architectural studies on lianas and hemiepiphytes have demonstrated that reiteration analysis provides the most relevant information for comparative studies between these two life forms (Caballé 1986, Caraglio 1986, Coudurier 1992, Delanoë 1992, Prósperi et al. 1995). Reiteration, the morphological process by which the plant reproduces in whole or in part its elementary architecture (Oldeman 1974, Barthélémy et al. 1989, Edelin 1991), is a phenomenon essential to the construction of a crown. Reiteration allows a plant to conquer new spaces, respond to local environmental conditions, and ultimately exploit the canopy (shoot reiteration) and the soil (root reiteration).

Reiteration is called delayed or differed when it leads to duplication of the architectural unit by means of latent buds. Delay varies considerably within a species and within an individual in relation to the most recently formed growth units. Sprouts and suckers are examples of delayed reiterated units. Sequential or immediate reiteration occurs concomitant with the process of tree development (Hallé & Ng 1981, Edelin 1984) and normally leads to crown construction.

Architectural analysis was conducted by observing living plants. For plants growing at soil level to about a few meters high, direct observation was sufficient. For larger plants, binoculars or a telescope were often necessary. Open sites in forests (e.g., tree-fall gap, forest edges,

hills or mounds, paths and roads) provided unobstructed views. Occasionally, free climbing or use of the Canopy Raft in French Guyana, Cameroon, and Gabon (Hallé & Pascal 1991) were necessary to gain access to tree canopies.

Drawing, an essential element of architectural analysis, permits the ordering and placing of data into a coherent ensemble. Typically we chose one or several informative angles of view. A rough draft captures the major features of the plant (e.g., trunk, branches and forks, principal root, or adventitious roots), respecting perspective and proportion. Then a scheme, drawn using binoculars (10 x 40), figures all axes in the same plane. Axes in front or in back of the plane are not represented, or they are indicated showing their insertion. Using a telescope, we then added the final details (FIGURE 1).

STUDY SITES

Our data result from more than 15 years of field study (1985–2000) in the intertropical zone of the Americas, Africa, and Asia. Work was conducted in all the major tropical forest types from dry forest to evergreen forest, and on continents as well as islands (such as Mayotte and Comoros). The greatest portion of these field studies was devoted to the study of lianas.

Geographic repartition and systematic value were determined by a review of existing literature. Taxonomic repartition was determined by a review of existing literature corrected and enhanced by the authors' field experience.

RESULTS

Geographic Distribution

Lianas

In north temperate primary forests, such as in Poland, Germany, and France, large-diameter lianas belonging to the genera *Vitis* (Vitaceae) and *Clematis* (Ranunculaceae) are encountered, but their representation in these forests is low to moderate (Gentry 1991). Southern temperate forests, notably the Valdivian forest, can be relatively rich in lianas; but the intertropical zone, particularly evergreen forests have the greatest diversity of lianescent species (FIGURE 2). The highest degree of diversity, recorded in South America, may be attributable to the diversity of the milieus in conjunction with geographic isolation (Prance 1987, Gentry & Dodson 1987, Gentry 1991). Conversely, the greatest number of individuals, or highest abundance, is found in Africa (Emmons & Gentry 1983, Caballé 1986, Gentry 1993) and may relate to the paleoclimate oscillation between hot and cold that took place



FIGURE 1. Illustration of different steps of architectural description. Different levels of simplification from a real plant to a schematic plant, here a *Ficus nympheifolia* (Moraceae, French Guyana).

during the Quaternary Period (Lanfranchi & Schwartz 1990, Sayer et al. 1992, Maley 1996). Insufficient data on Asian lianas prevents an evaluation of their repartition; however, Gentry (1991) gives some numbers for Australasia (lianas + hemiepiphytes >2.5 cm), suggesting an abundance similar to that of the neotropics.

Hemiepiphytes

Essentially inhabitants of tropical humid forest canopies (FIGURE 3), from sea level to 2500 m altitude (Williams-Linera & Lawton 1995), hemiepiphytes also may be found in temperate

forests of New Zealand, especially certain species of *Metrosideros*, Myrtaceae (Oliver 1930; Dawson 1966, 1967). Highest species diversity is found in Asia, reflecting that the center of diversity for the genus *Ficus* (Moraceae) occurs here (Corner 1958, 1967) and that many *Ficus* species are hemiepiphytes.

Taxonomic Distribution

One measure of success for a plant group's growth strategy is the group's importance in the colonized habitat; another is reflected in the de-

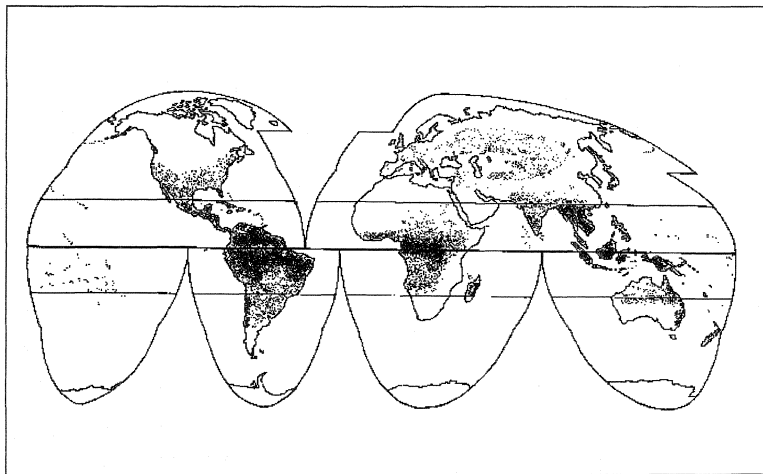


FIGURE 2. Geographic distribution of lianas.

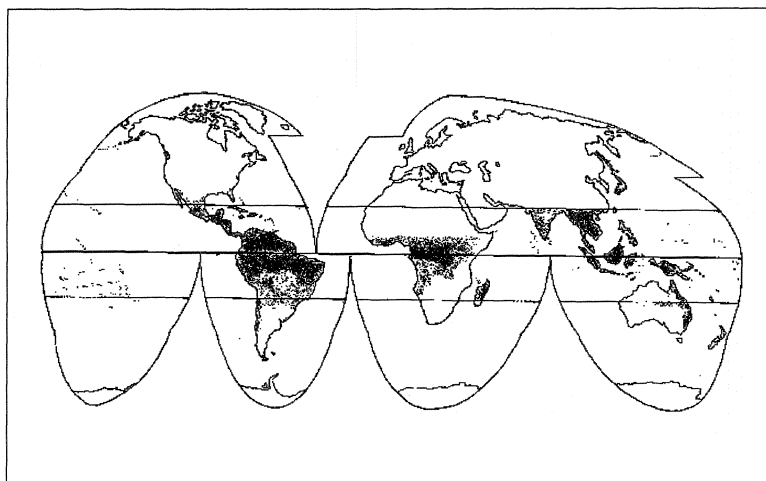


FIGURE 3. Geographic distribution of hemiepiphytes.

gree of species diversity. Many liana and hemiepiphyte families demonstrate these growth strategies, but we consider only the major taxa at the family and genus levels.

Lianas

The family with the largest number of liana species is Leguminosae with ca. 1100 spp., followed by Asclepiadaceae, Apocynaceae, Malpighiaceae, Bignoniaceae, Passifloraceae, and Hippocrateaceae (FIGURE 4). Typically Hippocrateaceae, Passifloraceae, Dichapetalaceae, and Bignoniaceae display a lianescent habit and have a high percentage of liana species (71%, 68%, 58%, and 50% respectively; FIGURE 5). Overall, about 30 families are rich in lianas (30% lianescent spp.). The palm family (Arecaceae), comparatively poor in lianas (20% of its spp.), contains *Calamus* (rattans), the largest genus of lianas (350 spp.). *Passiflora* (Passifloraceae), also

a very large genus (300 spp.), is in a liana-rich family (FIGURE 6).

Hemiepiphytes

The leading families with hemiepiphytes are Araliaceae, Cecropiaceae, Clusiaceae, Melastomataceae, and Moraceae (FIGURE 7). Unlike lianas, a single family, Moraceae, predominates, and this by virtue of a single genus, *Ficus*, with about 500 species (FIGURE 8). *Clusia* (Clusiaceae) ranks second in terms of numbers with about 85 species (FIGURE 9).

In summary, lianas evidently have a broader geographic repartition than hemiepiphytes primarily because of their presence in northern and southern temperate zones. Notwithstanding, it is in the inter-tropical zone that the two life forms achieve their greatest expression.

A large disparity exists in terms of species numbers between hemiepiphytes and lianas. Although different authors (see Gentry 1993) agree on a total of 20,000 climbers (including vines, lianas, and some hemiepiphytes), only 6000 are woody lianas, and woody hemiepiphytes number only 850 (TABLES 1, 2). A large number of angiosperm families have woody lianas (51), compared with the 28 families having woody hemiepiphytes. Although a single family, Moraceae, predominates among hemiepiphytes, several families have significant numbers of liana species. Conifers (Pinopsida) have no lianas or hemiepiphytes; but at a higher taxonomic rank, such as gymnosperms, lianas are present in the genus *Gnetum* (Gnetaceae), and Gnetaceae is primarily a lianescent family. No hemiepiphytic gymnosperms have been found. Among monocotyledonous angiosperms, besides the rattans

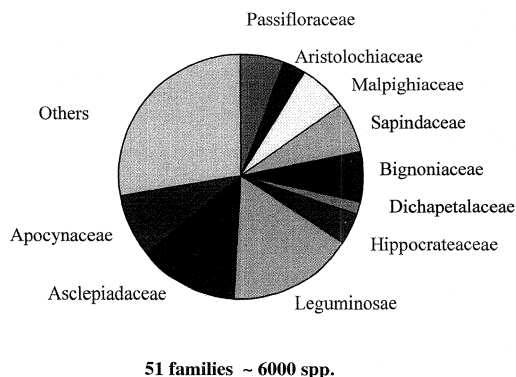


FIGURE 4. The most species-rich families of lianas.

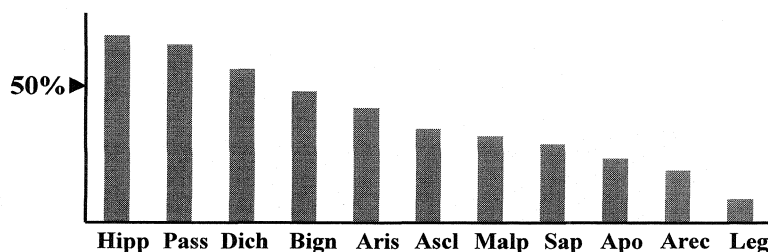


FIGURE 5. Liana families, with number of lianescent species as a percentage of the total species. Apo = Apocynaceae; Arec = Arecaceae; Aris = Aristolochiaceae; Ascl = Asclepiadaceae; Bign = Bignoniaceae; Dich = Dichapetalaceae; Hipp = Hippocrateaceae; Leg = Leguminosae; Malp = Malpighiaceae; Pass = Passifloraceae; Sap = Sapindaceae.

previously mentioned (*Calamus*, Arecaceae, and some other genera), the genus *Freycinetia* (Pandaceae) with about 175 species is exclusively lianescent. In the Araceae, the large genus *Philodendron* (ca. 300 spp.) harbors the only monocotyledonous hemiepiphytes (ca. 130 spp.).

Life History

Lianas are plants that germinate in the earth. When young, they are self-supporting, and their growth is relatively slow. A "search-for-support" phase is crucial for shoot establishment. Upon contact with a support, the plant undergoes an anatomical transformation associated with development of a host attachment system (FIGURE 10A).

Conversely, ascendance toward and into the canopy represents a period of rapid growth, but one with many "peaks" (e.g., *Tetracera alniifolia*, Dilleniaceae; Caballé 1980). Expansion and complete expression of the plant body in full sunlight is followed by the reproductive phase with flowering and fruiting (FIGURE 10B).

In parallel with host attachment and ascendance, a liana develops an adventitious root system that primarily performs a nutritional function, rarely an attachment one. Host attachment is usually by means of shoot modifications. In this manner, lianas, such as the genus *Entada* (Mimosaceae), can achieve sizes of 10–100 m, even up to 1 km long and more! Hemiepiphytes germinate on an aerial support. The resultant

seedling is small, develops a primary root system, and grows slowly at this stage. The primary root system is ephemeral but assures the nutrition and attachment, often in precarious positions, of the seedling.

Soon after the primary root system is elaborated, the seedling searches for the earth by means of a highly developed, rapidly growing adventitious root system (FIGURE 10C). Once contact is made with the soil, upward growth of the shoot system into the canopy begins (FIGURE 10D). Rapid elaboration of the root system by reiteration also occurs, leading to the expansion and complete expression of the root and shoot systems, without necessarily being in full sunlight. This is followed by flowering and fruiting (FIGURE 10E). Hemiepiphytes range in length from a few to 40 m.

Architecture

Crown construction

Lianas grow essentially by relay; that is, one module develops, the extremity dies, and another module takes over. According to Coudurier (1992), a typical liana module is made up of a dominant primary axis, the trunk, and reduced axillary formations. The principal axis can be either orthotropic with a twining or tendrilled distal portion or a mixed axis that is orthotropic proximally and plagiotropic distally. At the summit of the trunk, one or two reiterated complexes form, which will reiterate at their summit. The

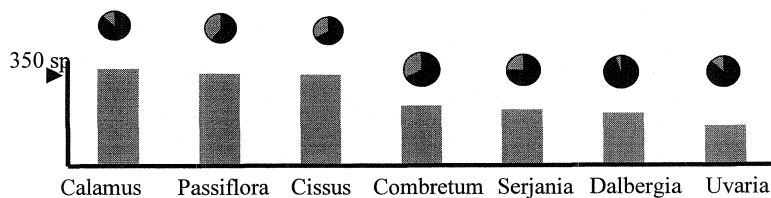
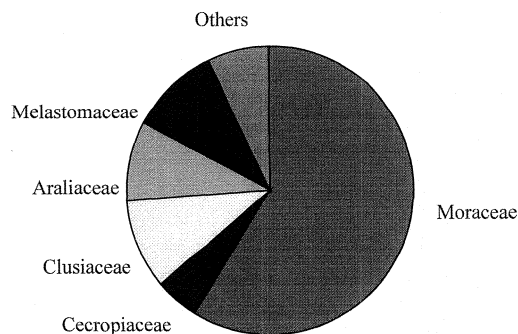


FIGURE 6. Liana genera, with bars representing the percentage of liana species in the family.



32 families ~ 850 spp.

FIGURE 7. The most species-rich families of hemiepiphytes.

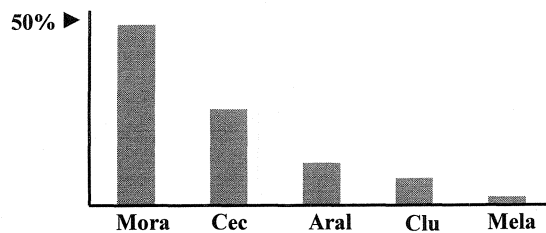


FIGURE 8. Importance of hemiepiphytes, with number of hemiepiphyte species as a percentage of the total species. Note: Mora = Moraceae; Cec = Cecropiaceae; Aral = Araliaceae; Clu = Clusiaceae; Mela = Melastomaceae.

TABLE 1. Families and genera including woody hemiepiphytes.

Family	No. hemiepiphytic spp.	Total spp. in family	Woody hemiepiphyte genera
Aquifoliaceae	1	420	<i>Ilex</i>
Araceae	133	2950	<i>Philodendron</i>
Anacardiaceae	3	850	<i>Rhus</i> , <i>Spondias</i>
Araliaceae	77	800	<i>Brassaiopsis</i> , <i>Pentapanax</i> , <i>Oreopanax</i> , <i>Polyscias</i> , <i>Pseudopanax</i> , <i>Schefflera</i>
Bignoniaceae	2	725	<i>Schlegelia</i>
Bombacaceae	4	250	<i>Ceiba</i> (syn. <i>Spirotheca</i>)
Burseraceae	1	540	<i>Bursera</i>
Cecropiaceae	45	200	<i>Coussapoa</i> , <i>Poikilospermum</i>
Celastraceae	2	1000	<i>Euonymus</i>
Clusiaceae	95	1350	<i>Clusia</i> , <i>Clusiella</i> , <i>Havetiopsis</i> , <i>Odematopus</i> , <i>Quapoya</i> , <i>Renggeria</i>
Cornaceae	3	90	<i>Griselinia</i>
Cunoniaceae	3	340	<i>Ackama</i> <i>Weinmannia</i>
Epacridaceae	1	400	<i>Dracophyllum</i>
Ericaceae	?	3350	<i>Cavendishia</i> , <i>Disterigma</i> , <i>Gaultheria</i> , <i>Gonocalyx</i> , <i>Rhododendron</i> , <i>Sphyrospermum</i> , <i>Vaccinium</i> , <i>Disterigma</i>
Loganiaceae	20	600	<i>Fagraea</i>
Melastomaceae	88	4750	<i>Adelobotrys</i> , <i>Bertolonia</i> , <i>Blakea</i> , <i>Dalenia</i> , <i>Dissochaeta</i> , <i>Medinilla</i> , <i>Miconia</i> , <i>Omphalopus</i> , <i>Topobea</i>
Moraceae	500	1200	<i>Ficus</i>
Myrsinaceae	?	1250	<i>Cybianthus</i> , <i>Embelia</i> , <i>Grammadenia</i> , <i>Rapanea</i>
Myrtaceae	?	3850	<i>Metrosideros</i>
Onagraceae	?	650	<i>Fuchsia</i>
Pittosporaceae	1	240	<i>Pittosporum</i>
Rosaceae	3	3100	<i>Pyrus</i>
Rubiaceae	?	10,400	<i>Coprosma</i> , <i>Cosmibuena</i> , <i>Hillia</i> , <i>Posoqueria</i> , <i>Schradera</i> , <i>Timonius</i>
Rutaceae	?	1700	<i>Zanthoxylum</i>
Sapotaceae	?	1100	<i>Sideroxylon</i>
Solanaceae	?	2600	<i>Markea</i>
Verbenaceae	1	1900	<i>Premna</i>
Violaceae	?	830	<i>Melicytus</i>

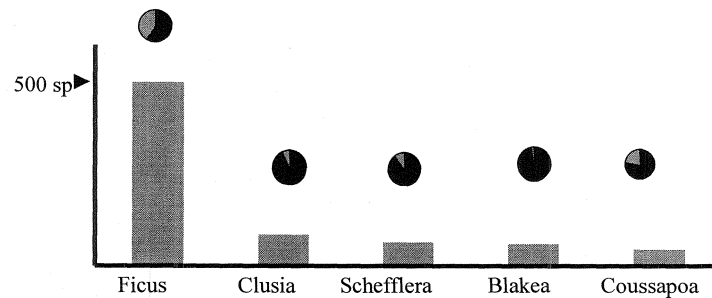


FIGURE 9. Hemiepiphyte genera, with bars representing the percentage of hemiepiphyte species in the family.

crown of a liana that reaches the canopy is thus formed of modules or superposed reiterated complexes (FIGURE 11). The trunk or base has large dimensions, and the crown is made up of progressively smaller units. Transformation to the lianescent life style—passage from a self-supporting to non-self-supporting adult—is accompanied by a number of remarkable and well-known architectural and anatomical modifications, collectively referred to as metamorphosis. Caballé (1993) wrote, “the aerial architecture and its development are directly affected by this change of state: growth is accelerated, internodes are elongated, climbing structures or mechanisms are established, the shape of leaves may be transformed completely and they can be arranged differently as phyllotaxy and branching characteristics are modified . . . (Prévost 1967, Cremers 1973, 1974, Huc 1975, Givnish & Vermeij 1976, French 1977, Etifier 1981, Blanc & Andraos 1983, Peñalosa 1983).”

Despite numerous and varied morpho-anatomical changes during liana development, overall crown construction is relatively uniform compared to that of hemiepiphytes.

Crown construction in hemiepiphytes primarily results from the modalities of sequential reiteration (Prósperi et al. 1995). Construction, which has an essential role in hemiepiphyte and host tree relations, determines the extension and form of the crown with which the hemiepiphyte will co-habit the support tree. We recognize three types of hemiepiphytic habit: arborescent, shrubby, and lianescent (FIGURE 12).

In species that present a single well-developed trunk with long, simple lateral branches, reiteration only serves to reinforce the basic architectural unit by developing supplementary axes in the crown periphery. The reiterative process also favors the horizontal spreading and extension of the hemiepiphyte, allowing it to grow above the crown of the support tree (e.g., *Clusia rosea*, Clusiaceae; *Ficus nymphaeifolia*, Moraceae). Such an essential apical growth confers to these hemiepiphytes an arborescent habit.

Alternately, in some species of *Clusia*, as well as *Coussapoa angustifolia*, *C. latifolia* (Cecropiaceae), *Dendropanax* spp. (Araliaceae), *Ficus guianensis* and *F. leiophylla* (Moraceae), reiteration is known to lead to a completely different occupation of space. Little growth of the trunk is accompanied by considerable basal reiteration. Such plants develop completely in the heart of the host tree's crown, competing with the support branches for light. Sequential basal reiteration, apparently a property offsetting this inconvenience, is the source of ramified groups of reiterated complexes that intercalate between the support branches. These groups are (1) either vertical ones such as in *Coussapoa*, where all reiterated complexes are vertical and which eventually can reach the top of the host crown (Caraglio in press); or (2) more of less horizontal ones as in *Ficus*, wherein the reiterated complexes fan out from the base into the available space. This mode of reiteration leads to a shrub-like habit (Caraglio 1986).

Lastly, hemiepiphytic species such as *Blakea* sp. (Melastomataceae) and *Clusia cuneata* (Clusiaceae) exhibit a third and most original manner of occupying space in the host. Self-supporting duplicated modules develop from the typically short trunk. Once these modules reach about 3–4 m and begin to get heavy, their self-supporting ability is compromised. This results in a sinuous trajectory wherein the long non-supporting modules multiply their points of attachment on the supporting branches of the host. Each reiterated complex grows up between openings in the crown branches and, in this manner, makes up part of a fragmented crown. This mode of reiteration recalls the strategy of lianas when they pass from the juvenile to adult stage (Coudurier 1992, Delanoë 1992).

Vegetative propagation

Vegetative propagation in lianas essentially concerns the shoot system (FIGURE 13A). All known modalities of vegetative propagation are expressed in lianas at different times during their

TABLE 2. Families and principal genera of woody lianas.

Family	No. liana spp.	Total spp./family	Principal woody liana genera
Acanthaceae	100	4300	<i>Thunbergia</i>
Actinidiaceae	25	355	<i>Actinidia</i>
Anacardiaceae	10	850	<i>Rhus</i>
Annonaceae	230	2050	<i>Artabotrys</i> , <i>Friesodielsia</i> , <i>Monanthotaxis</i> , <i>Popowia</i> , <i>Uvaria</i>
Apocynaceae	400	2100	<i>Forsteronia</i> , <i>Mandevilla</i> , <i>Landolphia</i> , <i>Melodinus</i> , <i>Odontadenia</i> , <i>Prestonia</i> , <i>Strophanthus</i>
Araceae	25	2950	<i>Monstera</i> , <i>Philodendron</i>
Araliaceae	10	800	<i>Schefflera</i>
Arecaceae	480	2650	<i>Calamus</i> , <i>Daemonorops</i> , <i>Desmoncus</i>
Aristolochiaceae	200	410	<i>Aristolochia</i>
Asclepiadaceae	800	2900	<i>Asclepias</i> , <i>Cecropegia</i> , <i>Gonolobus</i> , <i>Hoya</i> , <i>Oxypetalum</i> , <i>Secamone</i>
Asteraceae	147	21,000	<i>Gynura</i> , <i>Mikania</i> , <i>Montanoa</i> , <i>Mutisia</i> , <i>Senecio</i>
Bignoniaceae	75	725	<i>Adenocalymna</i> , <i>Anemopaegma</i> , <i>Arrabidaea</i> , <i>Memora</i>
Caesalpiniaceae	100	2000	<i>Bauhinia</i> , <i>Caesalpinia</i>
Capparidaceae	10	675	<i>Capparis</i>
Caprifoliaceae	25	365	<i>Lonicera</i>
Celastraceae	45	1000	<i>Loeseneriella</i> , <i>Tontelea</i>
Combretaceae	150	500	<i>Combretum</i>
Connaraceae	140	380	<i>Agelaea</i> , <i>Cnestis</i> , <i>Connarus</i> , <i>Rourea</i>
Convolvulaceae	140	1650	<i>Convolvulus</i> , <i>Ipomoea</i> , <i>Merremia</i>
Cucurbitaceae	15	760	<i>Cayaponia</i> , <i>Cucurbita</i> , <i>Gurania</i> , <i>Momordica</i>
Dichapetalaceae	75	180	<i>Dichapetalum</i>
Dilleniaceae	65	300	<i>Hibbertia</i> , <i>Davilla</i> , <i>Doliocarpus</i> , <i>Tetracera</i>
Dioscoreaceae	80	630	<i>Dioscorea</i>
Ephedraceae	5	40	<i>Ephedra</i>
Euphorbiaceae	140	7950	<i>Croton</i> , <i>Dalechampia</i> , <i>Macaranga</i> , <i>Phyllanthus</i> , <i>Tragia</i> , <i>Alchornea</i>
Gnetaceae	26	30	<i>Gnetum</i>
Hernandiaceae	12	68	<i>Illigera</i>
Hippocrateaceae	240	350	<i>Hippocratea</i> , <i>Salacia</i>
Hydrangeaceae	?	170	<i>Hydrangea</i>
Icacinaceae	20	320	<i>Iodes</i>
Linaceae	20	300	<i>Hugonia</i>
Loganiaceae	150	600	<i>Strychnos</i>
Malpighiaceae	295	1100	<i>Heteropterys</i> , <i>Banisteriopsis</i> , <i>Hiraea</i> , <i>Mascagnia</i> , <i>Stigmaphyllon</i> , <i>Tetrapteryx</i>
Melastomataceae	?	4750	<i>Gravesia</i>
Mendonciaceae	30	60	<i>Mendoncia</i>
Menispermaceae	100	520	<i>Abuta</i> , <i>Cissampelos</i> , <i>Stephania</i> , <i>Tilacora</i> , <i>Tinaspora</i>
Mimosaceae	320	3100	<i>Acacia</i> , <i>Mimosa</i> , <i>Entada</i>
Oleaceae	120	900	<i>Jasminum</i>
Pandanaceae	20	675	<i>Freycinetia</i>
Papilionaceae	615	11,300	<i>Dalbergia</i> , <i>Lonchocarpus</i> , <i>Machaerium</i> , <i>Millettia</i> , <i>Rhynchosia</i> , <i>Canavalia</i> , <i>Centrosema</i> , <i>Clitoria</i> , <i>Dioclea</i> , <i>Mucuna</i>
Passifloraceae	350	550	<i>Passiflora</i> , <i>Adenia</i>
Polygonaceae	70	1150	<i>Coccoloba</i>
Ranunculaceae	100	1750	<i>Clematis</i>
Rhamnaceae	29	875	<i>Gouania</i> , <i>Ventilago</i>
Rosaceae	40	3100	<i>Rosa</i> , <i>Rubus</i>
Rubiaceae	62	10,400	<i>Canthium</i> , <i>Manettia</i> , <i>Mussaenda</i> , <i>Randia</i> , <i>Sabicea</i> , <i>Tarenna</i> , <i>Uncaria</i>

TABLE 2. Continued.

Family	No. liana spp.	Total spp./family	Principal woody liana genera
Rutaceae	?	1700	<i>Zanthoxylum</i>
Sapindaceae	400	1350	<i>Paullinia</i> , <i>Serjania</i>
Schisandraceae	?	47	<i>Schisandra</i>
Smilacaceae	?	225	<i>Smilax</i>
Solanaceae	80	2600	<i>Solanum</i>
Verbenaceae	120	1900	<i>Aegiphila</i> , <i>Clerodendrum</i> , <i>Vitex</i> , <i>Petrea</i>
Vitaceae	400	800	<i>Cissus</i> , <i>Vitis</i>

life (Beekman 1981, Caballé 1994). Lianas exhibit terrestrial and aerial layering, transversal and longitudinal shoot fragmentation, stolons, flagella, basal shoot sprouts, and lignotuber formation.

The lianescent habit could not be achieved without a series of attachment points along one or more supports (Coudurier 1992, Putz 1995). If the extremity of a growing liana in the understory does not have a support, the shoot will touch the soil. The portion of the shoot in contact with the soil can continue to grow, root, ramify, and even split up. Over time, such layering is followed by splitting up of the shoot that leads to creation of new individuals or ramets (i.e., *Tetracera alnifolia*, Vitaceae, in Gabon; Caballé 1980).

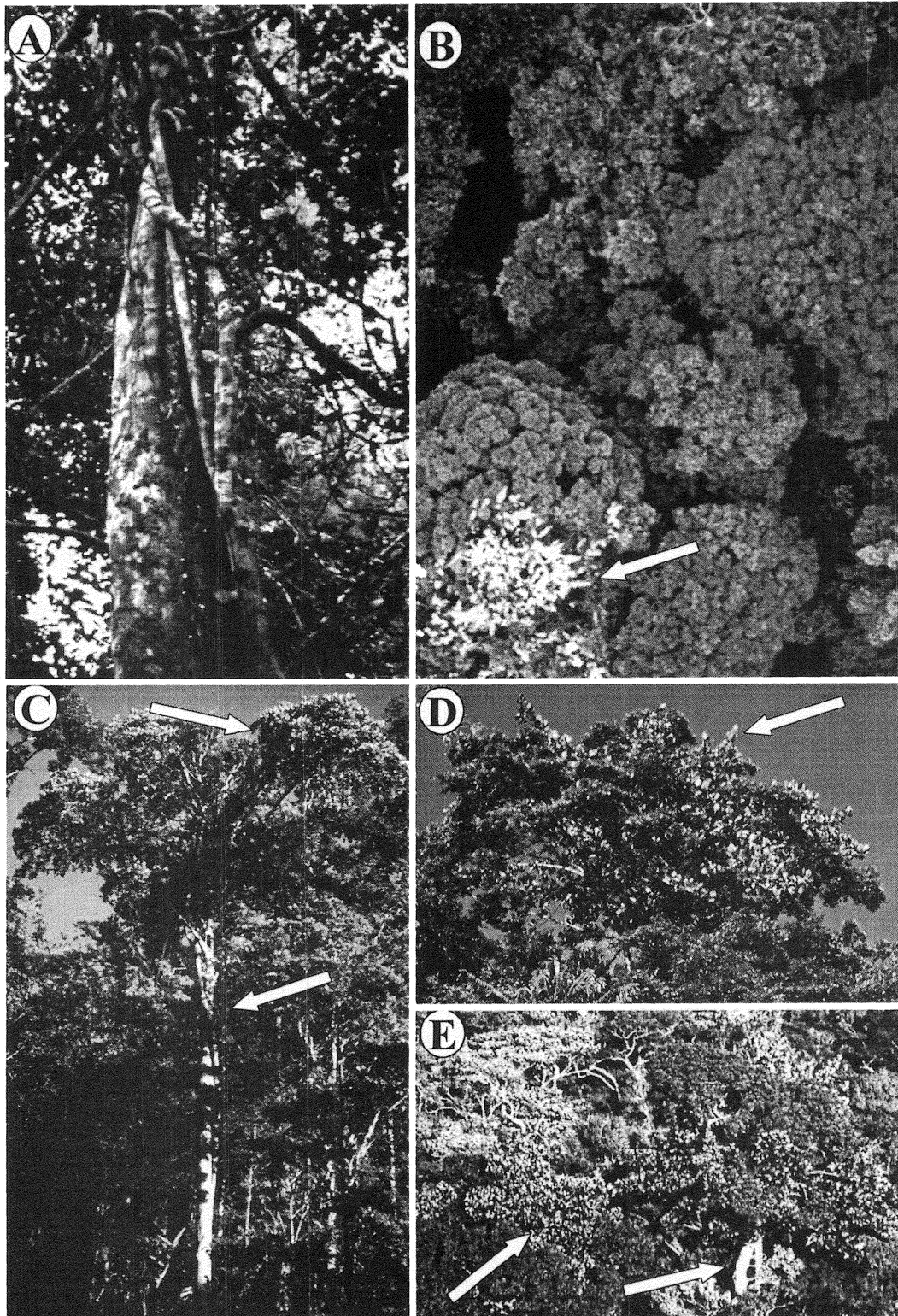
Longitudinal fissuring of the stem of adult lianas is common in several different families. Specific species that split in this manner include *Dalhousiea africana* (Fabaceae), *Cissus dinklagei* (Vitaceae), *Combretum mortehanii* (Combretaceae), *Landolphia* sp. (Apocynaceae), *Loeseneriella clematoides* (Hippocrateaceae), and *Millettia* sp. (Fabaceae) (Caballé 1994). In these plants, the whole anatomical structure of the shoot prefigures the cleavage lines, and hence the longitudinal fissures that lead to clone formation.

The biological significance of stolon formation by lianas is rarely discussed (Blanc & Andraos 1983). A stolon, a shoot that develops from an axillary meristem and grows horizontally along the ground, is often confused with organic understory debris. Liana stolons exhibit long slender internodes and rarely, petiolate leaves. Stolons have the capacity to form adventitious roots and to reiterate the young plant's shoot structure (e.g., *Arrabidaea inaequalis*, Bignoniaceae; *Doliciarpus* spp., Dilleniaceae; *Pacouria guianensis*, Apocynaceae; *Solanum terminale*, Solanaceae). In French Guiana, Coudurier (1992) concluded that their different modes of vegetative reproduction represented intermediary evolutionary steps toward stolon formation. He recognized the following steps:

the appearance of sprouts at the base of the plant, development of a horizontal branch and/or its dipping to the ground, and capacity to reiterate and thereby form a new organism at a distance from the parent plant. According to Coudurier, "the result of this tendency is the realization of horizontal structures of great size that permit vegetative multiplication at a distance." Araceae and Piperaceae lianas have specialized structures known as flagellas, which are very effective at propagating vegetatively. Flagellas result from morphological transformation of growing shoot apices; for example, an inflorescence (reproductive shoot) may be replaced by a vegetative shoot such as a branch. As Blanc (1980) explained "the effect of a flagella is to convert the apical meristem to a branch, and represents an exploration strategy and a method of defense for the plant in ecologically limited conditions." Flagellas correspond to occasional methods of vegetative multiplication, whereas stolons are a normal part of the differentiation of a lianescent plant.

Studies conducted on *Entada scelerata* (Mimosaceae) in Gabonese forests have demonstrated that it reproduces vegetatively by very particular mechanisms (Caballé 1977). At a late stage in the life of the liana, the main shoot in contact with the soil develops a structure similar to the parent root collar, forming a relay link at a dozen meters from the initial site of germination of the parent trunk. Gradually, the shoot segment between the parent and relay root collars degenerates, and the new root collar ("replacement collar") assumes the function of the parent collar. The shoot developing from the replacement collar represents a new, young structure, which consequently undergoes total reiteration. Development of a second root collar enables the resultant clone to explore and exploit the forest environment at a distance of 12 m from the parent plant.

To establish themselves and survive in an unstable milieu such as the canopy, hemiepiphytes have developed an opportunistic life style that essentially depends upon their capacity to prop-



agate vegetatively (Prósperi 1998b). This capacity is expressed in the formation of suckers, which occur with great frequency in the genus *Coussapoa* (Cecropiaceae), and layering, found in some *Clusia* (Clusiaceae) and widespread in *Ficus* (Moraceae). In *Coussapoa latifolia*, suckers develop along the principal or "tape" root (FIGURE 13B), which links the hemiepiphyte to the soil; in *C. asperifolia*, they develop from anchorage roots of the tape root. In *Clusia rosea*, suckers develop from aerial roots of basal branches and, at the soil level, emanate from the soil surface, spreading laterals of the tape root. With an organization similar to that of the parent plant, these suckers guard an autonomous character following fragmentation of the root from which they arose and development of their own adventitious root system, which provides anchorage, nourishment, and tape roots.

Layering in hemiepiphytes can be produced in the canopy or on the ground. In *Clusia cueneata* and *Ficus amazonica* observed in French Guiana and *Blakea* sp. and *Ficus maitin* studied in Venezuela, layering occurs upon contact of certain branches of the hemiepiphyte with those of the support (Caraglio 1985, Prósperi 1998a). Such layering allows these species to gradually colonize the crown of their host by means of multiple anchorage points. In *C. rosea*, layering begins with formation of large tape roots that, upon reaching the soil, assure the direct nutrition of the axis from which they derive. These roots are located on the proximal ventral portion of the lower branches and have a diameter similar to those of the trunk. They constitute root columns similar to the pillar roots of Banyan trees (such as *Ficus benghalensis*). Distal to the pillar, the branch augments in diameter and grows progressively upright until it constitutes a reiterated complex. In addition, the region between the branch proximal to the pillar and its insertion on the trunk forms a reiterate, ultimately becoming autonomous from the mother plant by gradual degeneration of the point of contact. In this way, a new individual is produced. This habit recalls a similar phenomenon well-known in tuft grass-

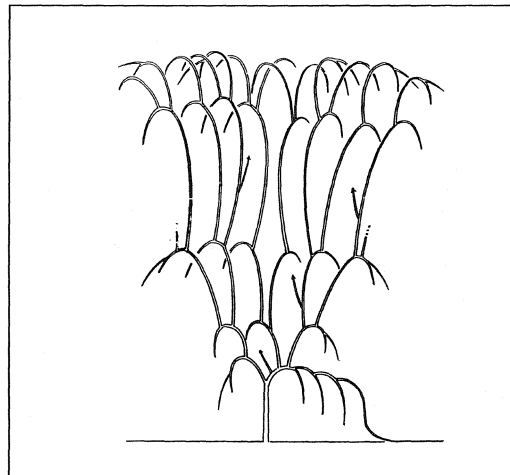


FIGURE 11. Crown building in Passifloraceae (from Delanoë 1992).

es (Poaceae) wherein the central portion dies, and the colony fragments and colonizes areas at a distance from the original site of parent seedling germination and establishment.

DISCUSSION AND CONCLUSIONS

The two biological types, lianas and hemiepiphytes, can be separated on the basis of several criteria (TABLE 3). An analysis of their development, particularly the manner of crown construction and vegetative propagation, indicates that the process of reiteration is of major adaptive importance to these plants as they compete for available space and to their survival in the forest. In a general way, sequential reiteration takes over in canopy expansion and exploration, whereas delayed reiteration comes into play in the survival of the organism as well as in its renewal (e.g., of damaged or destroyed parts).

For lianas, reiteration allows the plant to go through the difficult passages in the understory and then to explore the canopy by successive

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FIGURE 10. **A, B.** Lianas seen from the canopy and understory. **A.** Connaraceae liana and support tree, evergreen forest, Kouyi, Congo (Photos G. Caballé). **B.** *Combretum* (Combretaceae) liana in fruit, evergreen forest, Bélinga, Gabon. **C–E.** Hemiepiphytes as seen from the canopy and understory. **C.** Evergreen forest of French Guiana, profile showing a *Clusia* (Clusiaceae) growing on a host tree. The upper arrow indicates part of the *Clusia* crown and the lower arrow a large root encircling the support tree's trunk (Photo Y. Caraglio). **D.** *Clusia platystigma* (Clusiaceae) hemiepiphyte in evergreen forest, St. Elie, French Guiana; the arrow indicates *Clusia* branches with large shiny leaves are intercalated into those of the support tree (Photo Y. Caraglio). **E.** Two individuals of *Clusia* sp. (Clusiaceae) Creek Voltaire, French Guiana. The arrow at left indicates a part of the crown imbricated in that of the support tree; the arrow at right indicates the tape root and anchorage roots (Photo F. Hallé).

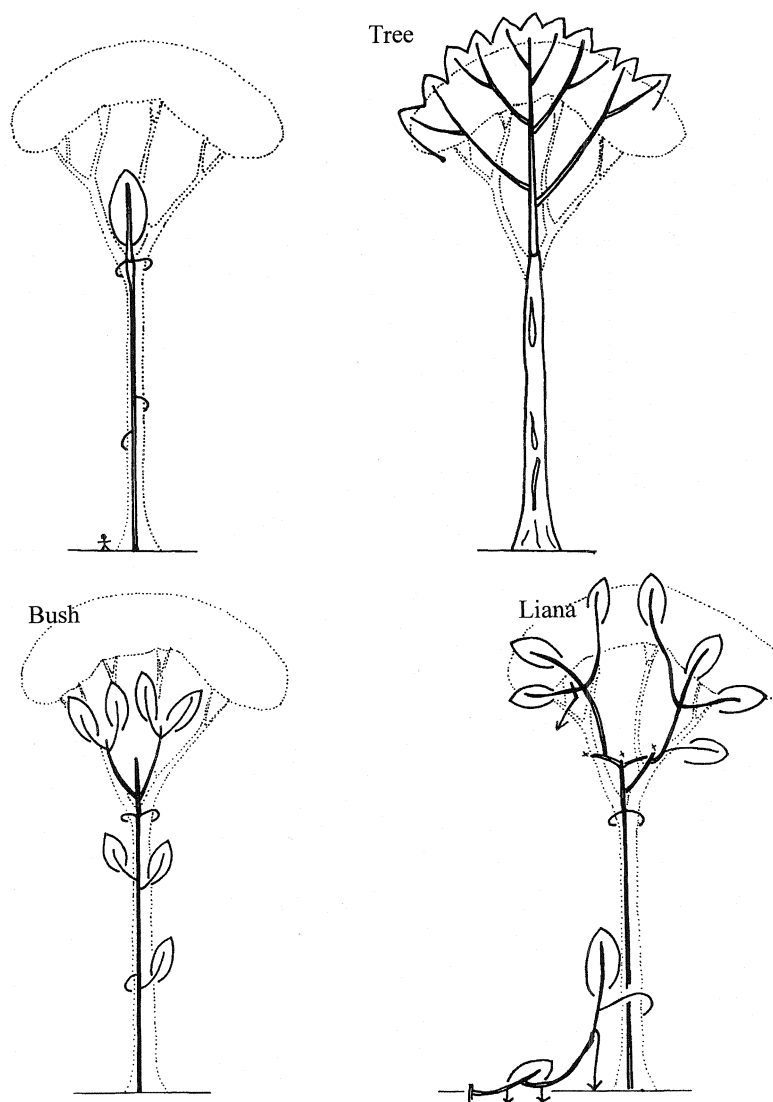


FIGURE 12. Crown building in hemiepiphytes. The young individual (upper left) can become a tree (upper right), a shrub (below left), or a liana-like plant (below right).

placement of reiterated complexes. Competition between a hemiepiphyte and its support also depends directly on its ability to reiterate. Depending upon their developmental potentials and opportunities in the canopy, hemiepiphytes occupy different volumes. When taking an arborescent form, the crown of the hemiepiphyte is more or less compact and can dominate that of the support. Shrubby or lianescent hemiepiphytes have a "discontinued crown" that is capable of intercalating between the support branches and occupying the available space at the interior or periphery of the host tree's crown.

Lianas and hemiepiphytes have developed a common "opportunistic" strategy based essentially upon their compartmentalization in forests. Their highly developed capacity to produce adventitious roots make possible a strategy, which, in turn, enables ensuing structures such as sprouts and layers to become autonomous individuals and, hence, clones.

Clonal growth is for hemiepiphytes and lianas an adaptive process essential to their survival because their habitat is precarious and depends upon the stability of the support tree(s) and/or the forest structure.

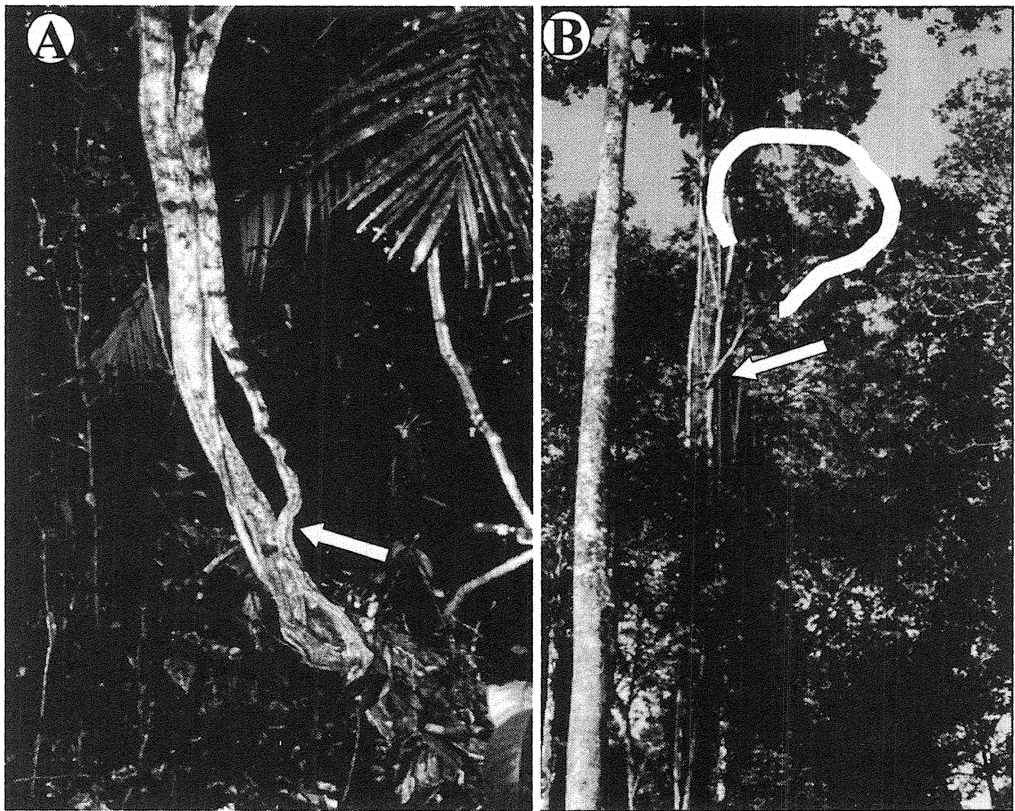


FIGURE 13. Vegetative propagation. **A.** Liana *Bauhinia* (Caesalpiniaceae), longitudinal fissuring of shoot, evergreen forest, St. Elie, French Guiana (Photo G. Caballé). **B.** Hemiepiphyte suckers developing from tap root of *Coussapoa latifolia* (Cecropiaceae), evergreen forest, St. Elie, French Guiana (Photo J. Prósperi).

TABLE 3. Main characteristics of woody lianas and hemiepiphytes.

Characteristics	Lianas	Hemiepiphytes
Taxonomic distribution	51 families	28 families
Geographic distribution	Pantropic and temperate areas	Pantropics
Development	Terrestrial germination Installation phase of shoot system Anchorage by leafy parts Crown building by stems stacking Not self-supporting except some juvenile stages	Epiphytic germination Installation phase of root system Anchorage by adventitious roots Edification by stems stacking Not self-supporting except some adult stages
Ecology	Vegetative propagation: Stem Reaching canopy from understory High response to environmental factors Disturbed areas Tree-fall gap, forest border, river edge Pioneers	Vegetative propagation: Root and stem Reaching canopy from lower canopy High response to environmental factors Stabilized areas Branch-fall gap, tree crown Pioneers

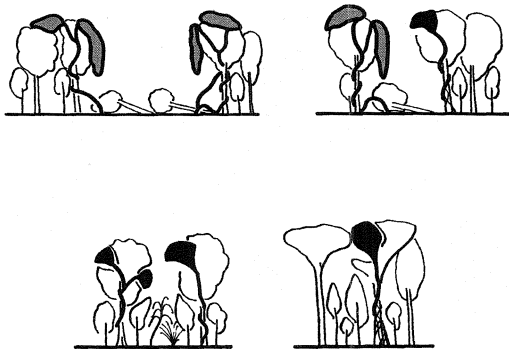


FIGURE 14. Forest profile showing how lianas and hemiepiphytes integrate into forest gaps such as this tree-fall gap, with lianas in gray (above), and hemiepiphytes in black (below).

Their different growth strategies, and especially vegetative multiplication, are a response to more or less violent environmental changes. Their capacity for growth (extension of lianas to reach light, adventitious rooting of hemiepiphytes to ensure survival) permits them to rapidly exploit free spaces. Their capacity to respond to light stimulation enables them to progress through the forest. In the elaboration of their architecture (competition between host and hemiepiphyte crowns and, for lianas, passage through different forest strata), response to light confers upon them a remarkable capacity to adapt to even strong variations in the forest ecosystem.

Lianas commonly occupy fragmented and disturbed forest zones (Putz 1984b), by reason of their terrestrial base and the force of their power to spread. Forest structural changes serve to stimulate their growth. On the contrary, a decrease in the occurrence of tree-fall gaps is following by a reduction of the liana population (Caballé & Martin 2001). Alternately, hemiepiphytes, with their aerial plant body and efficient modes of canopy occupation, act as binders of tree crowns. Ecologically, the two strategies complement one another. Together, they serve a protective and conservation function in the forest ecosystem by occupying and binding free space (FIGURE 14).

Our understanding of the cohabitation of lianas and hemiepiphytes in tropical forests is but nascent and should be enlarged (Gentry 1988, Faber-Langendoen & Gentry 1991). Architectural knowledge can help in making assumptions on adaptive traits that allow such plants to colonize or occupy particular status in the forest structure or dynamics. The architectural mechanisms of woody lianas and hemiepiphytes also

point out new ideas about growth habit evolution (i.e., trees versus lianas; see Putz 1980). An overall perspective of their biology should take into account aspects of ecophysiology (Holbrook & Putz 1996).

ACKNOWLEDGMENTS

The authors thank Dawn Frame for her very helpful translation of the paper. This is publication No. ISEM 99-110 of Institut des Sciences de l'Evolution, UMR 5554 du CNRS.

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